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V. N. Melnikov, K. P. Grudov, and A. Bitumba

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Analysis of diurnal vertical migrations of fishes

by V.N. Melnikov, K.P. Grubov and A. Bitumba

The efficiency of a mathematical model of the vertical migrations of fishes is shown. On the basis of this model, we discuss the nature and extent of the effect of various biotic and abiotic factors on the parameters of vertical migrations.

During certain periods of the annual cycle, pelagic fishes perform vertical migrations. A large number of papers has been devoted to analyzing the causes and characteristics of vertical migrations [1, 2, 5]. All of the authors note that a fish stays within a certain light intensity range during vertical migrations. This has served as a basis for the development of a mathematical model of the vertical migrations of fishes [3].

According to the model, the depth (H) at which a fish is found at a point in time (T) during vertical migrations (time is counted off from 12 noon) is determined by the formula

$$H = \frac{a\{\cos[15(T-12)]\cdot\cos\varphi\cdot\cos\delta_0 + \sin\varphi\cdot\sin\delta_0 + \sin h_1\} - \lg E}{\alpha_v}, \qquad (1)$$

where a is a coefficient which averages 9.0 on a clear day and 8.0 on a gloomy day, h_1 is the depth to which the Sun sinks (equal to 15°), at which the illumination of the water surface is conditionally accepted as 0, φ is the geographic latitude

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of the area (deg), δ is the Sun's declination (deg), α_v denotes the vertical decrease of light in the water (m^{-1}), and E denotes the intensity of illumination (lux).

The speed of the downward vertical migration of a fish is

$$v = \frac{7{,}4 \cdot 10^{-5} a}{\alpha_v} \cos\varphi \cdot \cos\delta_0 \cdot \sin[15(T-12)]. \qquad (2)$$

The height of the fish layer during vertical migrations is

$$H' - H'' = \frac{\lg \frac{E'}{E''}}{\alpha_v} = 1{,}4 X_s \cdot \lg \frac{E'}{E''}, \qquad (3)$$

where E' and E'' denote the upper and lower boundaries of the light range in which the fish is found during vertical migrations (lux), and X_s is the nominal transparency of the water measured with a Secchi disc (m).

The efficiency of the model and the effect of various factors on the parameters of vertical migrations are discussed in this paper.

The efficiency of the model was tested by comparing the actual parameters of vertical migrations with the estimated ones. The actual parameters of vertical migrations were established by analyzing the echograms of fish concentrations in the central E Atlantic and SE Atlantic. Over 400 echograms were analyzed. Published data on fish distribution during vertical migrations were also used [1, 4].

The very broad and only approximately established light range in which a fish stays during vertical migrations makes it difficult to test the model. The most reliable data on the efficiency of the model can be derived by comparing the actual and estimated velocities of vertical migrations, since they depend not on the absolute values of illumination, but only on its variation rate.

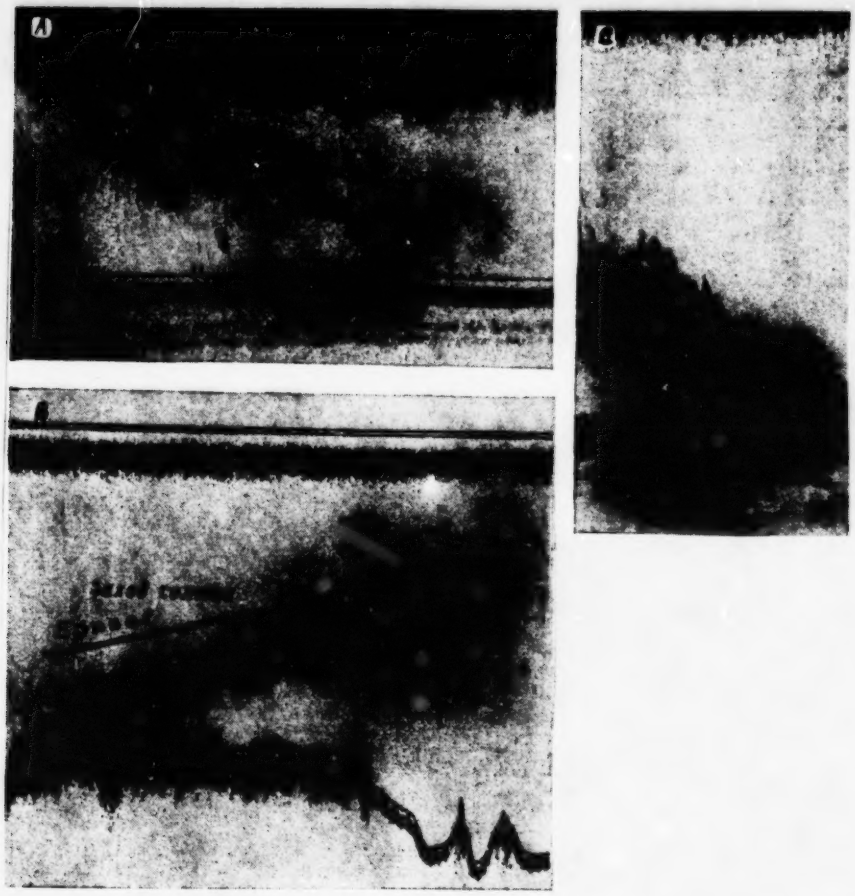

Fig. 1. Echograms of vertical migrations of scad in the SE Atlantic. A, B – during downward migration, C – during upward migration

Fig. 1 depicts the vertical migrations of scad in the SE Atlantic. For comparison, the echograms show lines with an inclination corresponding to the mean estimated velocities of vertical migrations derived by formula (2). For the given conditions, the estimated velocities of downward migrations were equal to 0.011 m/s. The difference between the actual velocity and the estimated one did not exceed 10-15% in any of the cases. The difference can be attributed not only to the approximate nature of the formula, but also to the insufficient accuracy of the water transparency data.

According to formula (3), the height of the fish layer during vertical migrations is directly proportional to the nominal transparency of the water X_S. Consequently, the accuracy of the design model can also be judged on the basis of the correlation between the height of the layer of a particular species of fish with the same E'/E" ratio and the transparency of the water. According to the data of V.K. Savrasov [4], approximately 80% of the scad concentrations in the NE Atlantic has a height of not more than 26 m. According to our own data, 80% of the scad concentrations in parts of the SE Atlantic have a height of less than 32 m, and in parts of the central E Atlantic a height of less than 42 m. Using the water transparency charts for the Atlantic Ocean, we have established that the mean vertical light reduction factor α_v is equal to 0.06 m^{-1} in parts of the NE Atlantic, 0.05 m^{-1} in parts of the SE Atlantic, and 0.04 m^{-1} in parts of the central E Atlantic. Therefore, the nominal water transparency in these areas averages 11.9, 14.3 and 17.9 m respectively. The ratios of the height of fish concentrations and water transparency in these areas are (110)

$$\frac{(H'-H")_{SEAt}}{(H'-H")_{NEAt}}=1{,}23;\quad \frac{(H'-H")_{NEAt}}{(H'-H")_{SEAt}}=1{,}31;$$

$$\frac{(H'-H")_{CEAt}}{(H'-H")_{NEAt}}=1{,}62;\quad \frac{X_{SEAt}}{X_{NEAt}}=1{,}20;\quad \frac{X_{CEAt}}{X_{SEAt}}=1{,}25;\quad \frac{X_{CEAt}}{X_{CEAt}}=1{,}50.$$

SEAt - SE Atlantic
NEAt - NE Atlantic
CEAt - Central E Atlantic

Good agreement of the results also points to the fairly high accuracy of the model of vertical migrations.

The efficiency of the model permits its use for the prediction of vertical migration parameters and analysis of the effect of various factors on these parameters.

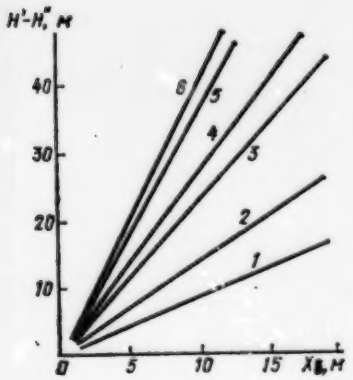

Fig. 2. Dependence of the height of the fish layer H'-H" on water transparency X_S for various light ratios at the upper and lower boundary of the fish layer: 1-5, 2-10, 3-50, 4-100, 5-500, 6-1000

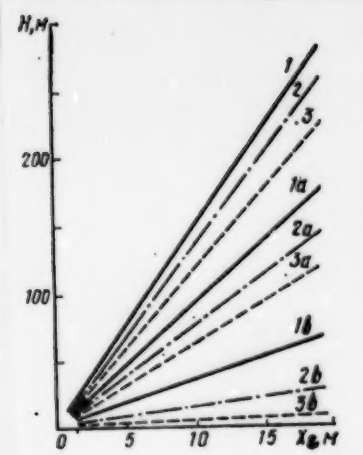

Fig. 3. Dependence of the depth of downward migration H on water transparency X_S for various local times T and the Sun's declination δ: 1,1a,1b - 20°; 2,2a,2b - 0°; 3,3a, 3b - 20°; 1-3 - T=16 h, 1a-3a - T=18 h, 1b-3b - T=20 h. Latitude of area 20°, threshold value of light intensity 10^{-3} lux, clear weather

The simplest thing is to determine the effect of various factors on the height of fish concentrations H'-H", which depends only on the nominal water transparency and the light range in the fish layer during vertical migrations. The results of our calculations of the H'-H" values by formula (2) for various X_S and E'/E" values are given in Fig. 2.

The nature of the effect of X_S on H'-H" does not require any special explanations. We can only say that the dissimilar transparency of the water in different regions of the world's oceans and inland bodies of water, as well as the seasonal and incidental variations in water transparency greatly affect the height of the fish layer during vertical migrations and in other cases, when the intensity of light in a body of water affects fish distribution. The broader the light range of the fish, the greater the effect of water transparency on H'-H".

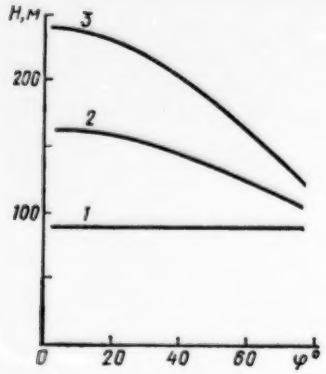

Fig. 4. Dependence of the depth of downward migration H on the latitude of the area for 12.00 hours (1), 16.00 hours (2) and 18.00 hours (3). Declination of the Sun 0°, vertical light reduction factor 0.06 m^{-1}, threshold value of light intensity 10^{-3} lux, clear weather

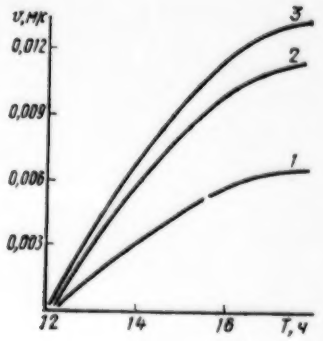

Fig. 5. Dependence of the velocity of vertical migrations v on the time of the day for latitudes 0° (1), 30° (2) and 60° (3). Declination of the Sun 0°, vertical light reduction factor 0.05 m^{-1}, clear weather

The width of the light range within the fish layer is affected by the flexibility of the sight organs of the fish, by the nonuniformity of the composition and size of the fish concentrations, and by the difference in the their biological and physiological condition. The data on the height distribution of fish concentrations can serve as an indication of possible variations in this range. According to our data, vertically migrating fish prefer to stay in the water level where the intensity of light does not vary more than 5—10-fold. With about 80% probability, the intensity of light in this layer varies less than 40—50-fold.

The depth of the downward migration of fish depends on the time of the day, the nature of the illumination at the water surface, the values of the light intensity kept to by the fish,

water transparency, the Sun's declination and the latitude of the study area.

Formula (1) was used to calculate the relationship between the depth of downward migration and the nominal water transparency at different times of the day (Fig. 3). Like the height of the fish layer, the depth of downward migration shows linear dependence on water transparency. Consequently, the relationship between the extent of vertical migrations and water transparency is also linear. The effect of the seasonal and incidental variations in the water transparency of a given area on the depth of the downward migration and the extent of the vertical migrations can be quite significant. In the shelf zone of the oceans where most of the commercial fishing is carried on, the transparency of the water may vary twofold and more throughout the year, even at fairly great distances from shore.

Naturally, the light conditions at the water surface do not affect the depth of downward migration as much as water transparency does. On a cloudy day, the intensity of light at the surface of the water is 2-5 times lower than on a clear day. Consequently, the fish keep to greater depths on a clear day, roughly X_S deeper than on a cloudy day. The light conditions also affect the time at which the vertical migrations begin and end, as well as the depth at which the fish are found at a certain time of the day.

The greater the latitude, the lower the Sun's position in the sky, the lower the intensity of light at the water surface and therefore the smaller the depth of downward migration at

the given time, and the smaller the maximum depth of downward migration during the day. The effect of the geographic latitude of the area on H is depicted in Fig. 4. The Sun's declination in a given area depends on the time of the year, and determines the height of the Sun's path across the sky. Even for a latitude of 20° (see Fig. 3), the effect of the Sun's declination on the depth of downward migration is quite significant. However, it is particularly great at higher latitudes. (112)

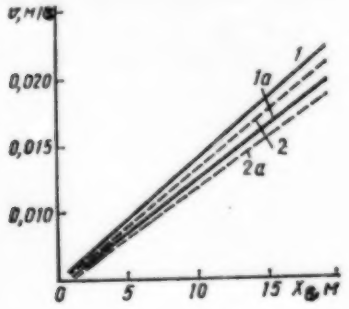

Fig. 6. Dependence of the velocity of vertical migrations v on water transparency X_S for different local times T and declinations of the Sun: 1,1a – 0°; 2,2a – ±23°; 1,2 – T=16.00 h; 1a,2a – 20.00 h

According to formula (1), the light intensity (E) to which a fish keeps during migrations has a significant effect on H. At the same time, it appears that the values of E are comparatively stable and lie within the 10^{-1}—10^{-3} lux range, at least for many of the pelagic fishes. Among other things, the narrow light intensity range in the fish layer during vertical migrations is an indication of small fluctuations in E.

The velocity of vertical migrations depends on the time of the day, the light conditions, water transparency and the latitude of the area. Velocity varies sinusoidally in relation to the first factor. The velocity of vertical migrations peaks immediately after the Sun rises and before it sets. Thus, the fish migrate at a greater speed in the surface layers, regardless of the direction of vertical migration (Fig. 5). The

velocity of vertical migrations is 8-10% greater on a clear day. Like the other parameters of vertical migrations, velocity shows a linear dependence on water transparency (Fig. 6).

The velocity of vertical migrations is greatly affected by the latitude of the area and the Sun's declination. Since the rate of light intensity variations at the higher latitudes is lower than in the equatorial zone during corresponding periods, the velocities of vertical migrations at the temperate and polar latitudes are generally smaller (see Fig. 5). According to formula (2), all other conditions being equal, the velocity of migrations peaks when the Sun's declination is equal to 0°, and decreases somewhat when it increases to $\pm 23^{\circ}$.

Thus, all the main characteristics of the vertical migrations of fish can be established by analyzing equations (1)-(3). We should keep in mind that the model of vertical migrations does not take into account the effect of the light that is reflected from the ground. The effect of this light is observed at a distance of up to 2-3 X_S from the bottom, and leads to a decrease in the vertical light reduction factor and the velocity of vertical migrations, and to an increase in the height of fish concentrations if the illumination at the bottom is not too intense.

Naturally, the actual parameters of vertical migrations may sometimes differ from the estimated ones under the effect of various abiotic and biotic factors.

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